Estonian Journal of Ecology, 2011, **60**, 2, 143–154 doi: 10.3176/eco.2011.2.05

Numbers and hybridization of spotted eagles in Estonia as revealed by country-wide field observations and genetic analysis

Ülo Väli

Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Riia 181, 51014 Tartu, Estonia; ulo.vali@emu.ee and Kotkaklubi, Valgjärve vald, Põlvamaa, Estonia

Received 20 December 2010, revised 8 March 2011, accepted 16 March 2011

Abstract. Spotted eagles include two medium-sized similar raptors breeding sympatrically in Estonia. In the current study I checked if population numbers derived from country-wide field observations over a 20-year period were in line with the estimate extrapolated from surveys in study plots (500–600 breeding territories of the Lesser Spotted Eagle and 10–30 territories of the Greater Spotted Eagle). I also analysed the structure of the hybridizing spotted eagle population using field descriptions and genetic analysis. The country-wide census enabled to distinguish 664 putative breeding territories, in 81% of which eagles were recorded in two or more years while in 53% breeding was confirmed. In 492 territories the species was identified in the field from morphological characters, and in 158 of them genetic analysis was used to verify the identification. The Greater Spotted Eagle was observed in 26 territories, in 54% of which breeding was confirmed. Altogether 10 pure-species Greater Spotted Eagle pairs and 14 pairs mixed with the Lesser Spotted Eagle were recorded whereas in 12 territories species compositions changed – mainly towards hybridization and Lesser Spotted Eagle pairs. Genetic analysis suggested breeding of an adult hybrid spotted eagle in eight territories and later generation backcrosses in five territories. The present study supported the plot-based estimates of population size but also showed extensive, partly hidden hybridization and decline of the Greater Spotted Eagle. It also showed that, despite several caveats, full census based on a large database of casual field observations can be a powerful tool for estimating the size and distribution of a rather numerous raptor population and is essential for discovering breeding sites of a rare species. In hybridizing species, however, more specialized approaches (comprehensive search of nests, detailed morphological descriptions, and genetic analysis) should be used as well.

Key words: *Aquila clanga*, *Aquila pomarina*, census, genetic analysis, hybrid, population size, raptor.

INTRODUCTION

Monitoring bird populations requires precise estimation of their numbers. In principle, this could be done in two ways. In the case of common species the estimates obtained in small study plots can be extrapolated to a larger area of interest, whereas rare species should be censused directly (Bibby et al., 2000; Gregory et al., 2004). Although the same approaches are used in birds of prey, their monitoring poses problems because of their low densities over extensive areas and use of specific habitats (Bibby et al., 2000; Hardey et al., 2009). For

most birds of prey a special monitoring programme is required, which, in order to obtain a sufficiently large sample size, should include many large study plots and intensive fieldwork, and thus sets high demands to people involved (Saurola, 1986). Quantitative population estimates of rare raptor species, such as most eagles, should rely on complete counts only, sometimes corrected later, e.g. according to the composition of the landscape.

An obstacle in monitoring can be the co-occurrence of several similar and/or closely related species in the same area. Morphological similarity creates identification problems while relatedness could mean the breakdown of the reproduction barrier and the interbreeding of species. Hybrids are difficult to identify on the species level (e.g. Lint et al., 1999) and – if fertile – they may produce backcrosses and later-generation hybrids that are even more difficult to identify (Allendorf et al., 2001). Ultimately, introgressive hybridization may lead to the occurrence of a hybrid swarm (continuous gradient of individuals from one species via all classes of hybrids to another species), raising questions as to the species' identity (Coyne & Orr, 2004; Price, 2008). Hence, if a mixed hybridizing population of two or more species coexists, monitoring requires additional efforts and, possibly, introduction of advanced methods, such as genetic analysis (Allendorf et al., 2001; Schwartz et al., 2007). Genetic monitoring of threatened species can be done in a non-invasive way, e.g. by collecting feathers moulted by adult birds at nest sites (Lõhmus & Väli, 2004; Rudnick et al., 2005).

The Greater Spotted Eagle *Aquila clanga* Pall. and Lesser Spotted Eagle *A. pomarina* Brehm are Eurasian raptors of conservation concern with distributions overlapping in eastern Europe. These medium-sized monogamous birds are sparsely distributed as solitary pairs (Cramp & Simmons, 1980). They are long-lived, with a generation time of some 11 years, and pair bonds are stable (BirdLife-International, 2004; Meyburg et al., 2005). Both species inhabit mosaic landscapes (Cramp & Simmons, 1980; Väli & Lõhmus, 2000; Väli, 2003): they nest in forest, but hunt over open landscapes where they are rather easy to spot for human observers. Although the preferred habitats somewhat differ between the species, a general overlap in habitat use, behavioural similarities and, most importantly, rarity of the Greater Spotted Eagle have resulted in interbreeding (Lõhmus & Väli, 2001, 2005; Väli, 2005). Indeed, in most of its European range the Greater Spotted Eagle is rare while the Lesser Spotted Eagle may reach rather high densities (Meyburg et al., 2001). Hybridization, as well as similarity of the species in several respects, makes the monitoring particularly difficult.

In Estonia, the first general estimates of the abundance of spotted eagles in the early 20th century described the Lesser Spotted Eagle as a widespread and the Greater Spotted Eagle as a rare species (Härms, 1927; Kumari, 1954; Lepiksaar & Zastrov, 1963). The first quantitative estimates, based on country-wide field observations, were given in the middle of the 20th century and reached up to about 100 pairs (Randla, 1976, 1985; Randla & Õun, 1983). More systematic research started in the late 1970s with the compilation of the first Estonian Bird Atlas (Renno, 1993). Then the estimates for the Lesser Spotted Eagle were increased two to three times (Lilleleht & Leibak, 1993; Tammur, 1994; Volke, 1996). In 1997,

the first large-scale survey based on data collected in study plots with differential extrapolation for four Estonian eco-regions resulted in further doubling the estimates to 480–600 pairs (Lõhmus, 1998). The same numbers have been obtained in two subsequent similar surveys in 2002 and 2008 (data by Kotkaklubi (Eagle Club), cited in Elts et al., 2003, 2009). Breeding of the Greater Spotted Eagle was not confirmed by the Bird Rarities Committee until the mid-1990s (Lõhmus, 1996). Its population size, based on the ratio between the two spotted eagle species in study plots, was estimated at 20–30 breeding territories in 1997 (Lõhmus, 1998). Later, the estimate has been reduced to 10–20 territories due to a decline in numbers (Elts et al., 2009; Väli et al., 2011).

In the current study, I summarize the observations of spotted eagles made in Estonia in 1991–2010. The first objective is to check whether such an attempt of full census could result in a reliable population estimate for a relatively common raptor and give the same outcome as extrapolations from surveys in study plots. Secondly, I present the number of pure-species pairs, hybridizing pairs, and hybrids found in Estonia, using field descriptions and genetic analysis. Such detailed information of an entire mixed-species spotted eagle population enables to explore current numbers and future perspectives of the globally vulnerable Greater Spotted Eagle in Estonia. For this species, found in very low numbers unevenly over the country and hybridizing with the Lesser Spotted Eagle, extrapolation of data from sample plots is not sufficient.

METHODS

The dataset included observations from all over Estonia made in 1991–2010. Most of the information came from the monitoring reports and unpublished records of the Nature Conservation Society Kotkas (the Eagle) and Kotkaklubi, including observations made in special study plots (5–7 plots, ca. 3000 km^2 in total). As many as 92.8% of the territories (incl. all the considered territories of the Greater Spotted Eagle and hybrids) were discovered or checked by the members of Kotkaklubi who have focused on locating eagle nests and study spotted eagles in detail. These data were supplemented by observations deposited in the databases of the Kabli bird station, Estonian bird atlas (2004–2009), eBiodiversity (http://elurikkus.ut.ee), Nature Observation Database (http://eelis.ic.envir.ee/lva/LVA.aspx#), Finnish Estonian Birding Society, and obtained via direct communication with people. These supplementary data mainly added occupation years to known territories.

Field identification of adult birds was based on morphological characters as suggested by Forsman (1999) and Svensson et al. (1999) and confirmed in the field by examination of genetically analysed birds. Nestlings were identified using morphometrics and plumage characters (see Väli & Lõhmus, 2004). As spotted eagles are hard to tell apart, regarding species identification I only considered as reliable well-described field observations, available photographs, and records of the instructed members of Kotkaklubi, each of them verified in interviews.

For the genetic analysis, blood samples and plucked feathers of nestlings, as well as moulted feathers of adults, were collected. The identification procedure combined microsatellite and single nucleotide polymorphism markers (Väli et al., 2010b) with mitochondrial DNA data indicating the maternal line (Väli, 2002). A special effort was made to collect and analyse genetic samples from all actual or suspected territories of the Greater Spotted Eagle and hybrids. The species composition of pairs may also change due to the replacement of birds. Territories of such pairs were considered as the same when summing up the total number of territories but considered separately in each category when counting species' numbers separately.

Estonia is a flat lowland (highest point 318 m), about 50% of which is covered by mosaic forests. Spotted eagles are distributed across the mainland (ca. 31 500 km^2). Although at least eight observations were made on Saaremaa Island and one on Kihnu Island in 1991–2010, these observations did not suggest breeding and were excluded from further analysis. In order to exclude migrating birds, only observations between 15 April and 15 August were considered as evidence of a breeding territory (but that being proven, other records were also taken into account). According to the field observations in Estonia (Ü. Väli & J. Tuvi, unpubl. data) and telemetry studies in Latvia (Scheller et al., 2001), territorial spotted eagles mostly stay within 2 km from the nest, although hunting flights may extend up to several kilometres (as far as 16 km). According to the data from a well-studied plot in east-central Estonia, the average distance between two active nests is about 3.4 km, while the shortest recorded distance in Estonia is 720 m (J. Tuvi, unpubl. data). In the current study, I used a conservative approach and observations less than 2 km from each other were considered as from the same territory unless nest findings proved otherwise. Records of subadults and obviously nonterritorial birds were excluded from the data set. Territories were initially grouped into six classes, which later were reclassified in three categories indicative of breeding probability: 'possible breeding' (single records of a bird in a year), 'probable breeding' (nest decorated with green branches, pair recorded, or single bird seen repeatedly during a year), and 'confirmed breeding' (nest with eggs or eggshells, nestling, brancher or recently fledged – and still being fed – juvenile).

RESULTS

In 1991–2010, altogether 3195 'territory occupation years' (sum of yearly recorded territories) from 664 putative breeding territories of spotted eagles were recorded (Fig. 1). Annually eagles were observed on average in 160 ± 86 (mean ± SD) territories and active nests were found in 84 ± 50 territories. Coverage of the breeding population increased from 84 ± 36 territories and 39 ± 15 nests in 1991–2000 to 236 ± 40 territories and 128 ± 25 nests in 2001–2010; the proportion of territories with known nests was relatively high and remained stable in both decades (51% ± 7%; Fig. 2). Of all territories, 52 (8%) were recorded only in

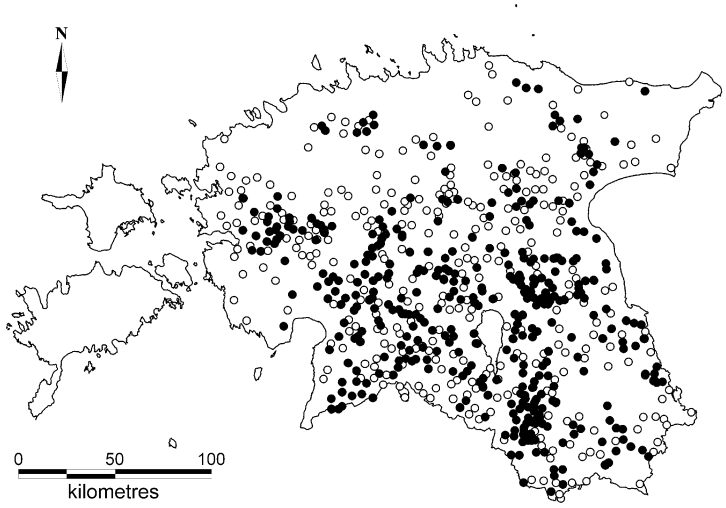

Fig. 1. Distribution of putative breeding territories of spotted eagles in Estonia in 1991–2010. Black dots indicate territories where nests have been found, white dots are territories without nest-finding.

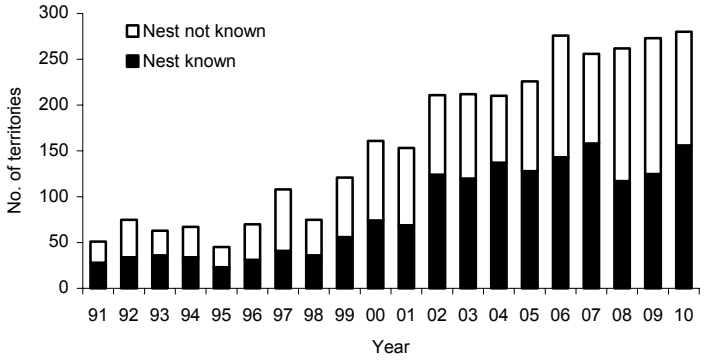

Fig. 2. Numbers of putative breeding territories of spotted eagles recorded in Estonia in 1991–2010.

1991–2000, 352 (53%) only in 2001–2010, and 260 (39%) in both periods. In 535 (81%) of the territories eagles were recorded in at least two years (Fig. 3).

Confirmed breeding was registered in 349 territories (53%; 338 territories with nests where breeding was recorded, 11 with only a juvenile observed), probable breeding in 170 territories (26%; 37 with a 'decorated' nest, 95 with a pair recorded, 38 with repeated sightings of a bird), and possible breeding in 145 territories (22%). However, in 68 'possible' territories single observations of a bird were made in two or more years. Breeding of the Greater Spotted Eagle was confirmed with nest-findings in 14 territories (54%), a pair was seen (probable breeding) in

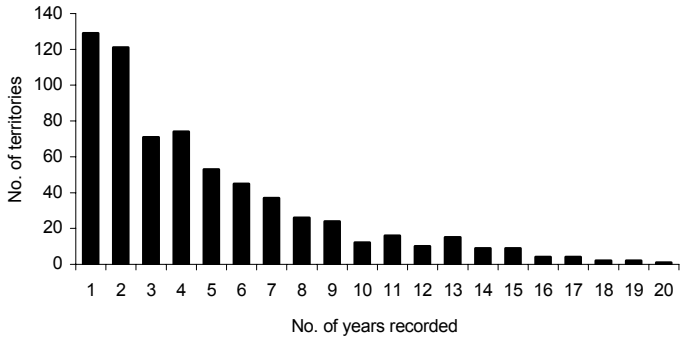

Fig. 3. Recording frequency of spotted eagle breeding territories in Estonia in 1991–2010.

eight territories (31%), and in four territories (15%) a single adult bird was recorded (possible breeding).

In 492 territories (503 when including pairs with switched species composition), the species was identified in the field by morphological characters and in 158 (177) of them the species identification was confirmed by genetic analysis. In addition to the pure-species pairs and mixed pairs of Greater and Lesser Spotted Eagles (Table 1), genetic analysis indicated breeding of an F1 hybrid eagle in eight territories (in seven pairs the partner was a Lesser Spotted Eagle and once another F1 hybrid) but only in four of them the adult hybrid was recognized in the field. One adult backcross (offspring of a hybrid and a Lesser Spotted Eagle) was trapped in the field whereas genetic analysis suggested breeding of four additional similar backcrosses. Nine territories of the Greater Spotted Eagle (five pure-species pairs, three mixed pairs, one with only an adult recorded) were abandoned during the study period, while six territories (two Greater Spotted Eagle pairs, four mixed pairs) were replaced by Lesser Spotted Eagle pairs; the latter happened also to

Table 1. Numbers of the Lesser Spotted Eagle, Greater Spotted Eagle, and mixed-species territories with various description level in Estonia in 1991–2010 based on morphological (M) and genetic (G) characters. Territories with switched species composition are included in each category involved

	Lessers		Greaters		Greater × Lesser	
	M	G	M	G	M	G
Two adults and nestling	118	2	4	2	11	6
One adult and nestling	76	13	0	1	1	6
Nestling	24	140	0	0	0	0
Two adults	89	0	6	0	2	0
One adult	166	6	6*	1	0	0
Total	473	161	16	4	14	12

* May include mixed-species (Greater × Lesser) pairs.

four pairs with an F1-hybrid involved. In 2010, there were six known territories of the Greater Spotted Eagle (including three mixed pairs and two pairs in need of further study on species composition) and in five sites presence of the species still needs verification.

DISCUSSION

In the current study, the population estimates of extensive country-wide field observations from 1991–2010 were generally similar to the results obtained by extrapolation of data collected in study plots: 500–600 pairs of the Lesser and 20–30 pairs of the Greater Spotted Eagle (Lõhmus, 1998; Kotkaklubi, unpubl. data). This increases the reliability of these figures. Earlier observation-based approaches have resulted in much lower estimates for the Lesser Spotted Eagle: some 100 pairs in the 1950s, 50 pairs in the 1960s, and 30–40 pairs in the 1970s (Randla, 1976, 1985; Randla & Õun, 1983). After the compilation of the first Estonian bird atlas the estimates were reset at 150–200 (Volke, 1996) and 200–300 pairs (Lilleleht & Leibak, 1993; Tammur, 1994), which were still less than half of the current estimation. Surprisingly, the earlier estimates for the Greater Spotted Eagle, although based on insufficient detail, were not much different: the species has always been considered as rare (sometimes as a breeder; Härms, 1927; Kumari, 1954; Lepiksaar & Zastrov, 1963) with a population size between 5 and 10 pairs (Randla, 1985) or 10–20 pairs (Randla, 1976).

Although the numbers of the Lesser Spotted Eagle may have changed to some extent (Lõhmus & Väli, 2001), the earlier estimations undoubtedly did not reflect the real population size. One reason for the earlier underestimation is that ornithological activity was significantly lower, especially in the first half of the 20th century (Renno, 1974; Mänd, 1992). Previously collected data were also less accessible as records often remained in observers' notebooks whereas nowadays many observations are deposited in freely accessible internet databases. Moreover, in the past some regions were underrecorded. For instance, raptors in south-eastern Estonia – the stronghold of the Lesser Spotted Eagle – were not much studied until the 1980s (Randla, 1976; Lõhmus & Väli, 2001). Fieldwork for the first Estonian bird atlas, conducted in 1977–1982 (Renno, 1993), initiated systematic country-wide data collection of all bird species. Similarly, the data for the second atlas, based on fieldwork in 2004–2009, improved the coverage of territories for the present study. Yet such wide-ranging general surveys may still provide poor information on particular species. Indeed, special spotted-eagle studies (Volke, 1996; Lõhmus, 1998) gave much higher estimates. The importance of focused research is also illustrated by the present study where the proportion of territories with known nests was high and stable (Fig. 2) and many territories were visited repeatedly (Fig. 3).

An important reason impeding population size estimation is poor knowledge of the species' biology and relevant identification features. In spotted eagles, only intensive search for nests, detailed observations, and telemetry studies have revealed the small size of their breeding territories (Scheller et al., 2001; Väli et al., 2004; Kotkaklubi, unpubl. data). Earlier views on all eagles as raptors with large territories

probably caused underestimation of population size. New identification guides (e.g. Forsman, 1999; Svensson et al., 1999) have improved raptor identification skills, with a concomitant increase of spotted eagle records. Recent comparative studies selecting characters for species identification (Bergmanis, 1996; Väli & Lõhmus, 2004; Dombrovski, 2006; Lontkowski & Maciorowski, 2010) have helped to identify Greater Spotted Eagles and to discover hybrids.

The current study also had some potential methodological caveats leading to an overestimation of the population size. Most importantly, although an observation of an eagle in the breeding season appeared to be a good indicator of a breeding territory (as most sightings were repeated and resulted often in nest-finding), not every observation is made of a territorial bird. In addition to breeders, each raptor population includes also non-breeding birds (Steenhof & Newton, 2007; Hardey et al., 2009). Their proportion can be rather high (Newton, 1985; Kenward et al., 2000), but estimating the size of this fraction, especially non-territorial (floating) birds, is difficult (Newton & Rothery, 2001; Hardey et al., 2009). Subadult Lesser Spotted Eagles (long-distance migrants) probably return less often to natal areas than shorter-distance migrant Greater Spotted Eagles, although subadults of both species have been recorded in the breeding ranges (e.g. Meyburg et al., 2005). Recent satellite telemetry studies have shown that they even can hold a territory for some time. For example, a young Greater Spotted Eagle hatched in Estonia returned after wintering in Spain to Estonia and spent its second and third summer in various Fennoscandian countries, staying at a site for several weeks in a row (Kotkaklubi, unpubl. data). Secondly, long-term surveys in study plots show that breeding territories may change in time and space, as shown by preliminary results from the Tartu study area where 69% of 29 territories were occupied permanently in the course of ten years while others were lost, added, or occupied only temporarily (Ü. Väli, unpubl. data). Additional studies are needed because the Tartu area has been harbouring several pairs of the Greater Spotted Eagle (Väli & Lõhmus, 2000), and the loss of territories is part of the country-wide decline of the Greater Spotted Eagle population (Väli & Lõhmus, 2000; Väli et al., 2010a, 2011). However, the current twenty-year study undoubtedly included some temporary breeding territories.

Several figures indicate that although the records from the two decades may include non-territorial birds and temporary territories these are not prevailing and do not obstruct general conclusions made in the current study. Repeated records of eagles in more than one year in 81% of the territories, as well as records from both studied decades from 39% of the territories (despite lower observational activity in the 1990s; Fig. 2), suggest that a high proportion of the discovered territories are consistently occupied in Estonia. The same was suggested by the proportion of the territories (78%) where breeding was confirmed or probable, and additional 10% of the territories where observations of single birds were made in two or more years. Many territories where a bird or a pair has been seen only once have not been visited by observers again later, although the territories could have stayed occupied by eagles. Finally, the regions of the country that showed the highest density of spotted eagles (Fig. 1) are, in fact, monitoring plots of spotted eagles, indicating that the current extensive country-wide survey

undoubtedly did not reveal all territories. This is not surprising because birding and ornithological activity in Estonia is still low compared to the countries in Northern and Western Europe for instance, and spotted eagles are not always easy to detect in the field. Moreover, some pairs may occupy territories for only a few days or weeks, which makes registration difficult (Steenhof & Newton, 2007).

Detailed examination of country-wide casual records of spotted eagles, followed by intensive field research, has added significantly to the knowledge of the numbers, distribution, and hybridization of the strictly protected rare Greater Spotted Eagle in Estonia. The 26 territories (14 with nests found) discovered in the course of two decades, however, do not reflect its current numbers as many territories were abandoned during the study period and only a few are retained at present. In monitored territories several switches in the species composition and frequent hybridization were noticed, with mixed-species pairings often being an intermediate step (see Väli et al., 2010a). Thus, seeing a Greater Spotted Eagle may be less common than seeing a hybrid in the western limit of the species' range and any observations of that species need close examination using photographs, detailed descriptions, or genetic analysis.

To sum up, a large number of field observations can give a rather good estimation of a sparse raptor population with up to 500–600 pairs even in a country with rather modest ornithological activity. In densely human-populated countries and/or those where bird-watching is at a higher level, probably even more numerous species can be censused in full. If available, a database of casual observations is definitely worthy of usage, even when it includes some identification errors. Obviously, extrapolation from random study plots is a cost-effective alternative for estimating population size and monitoring population dynamics. However, rare species, such as the Greater Spotted Eagle, cannot be studied in small study plots, whereas the current approach revealed the small size of the population at present, as well as its rapid decline and extensive hybridization. Moreover, country-wide fieldwork resulted in the discovery of many nest sites of both spotted eagle species and helped to organize their protection. Hence, in hybridizing spotted eagles, the collection of country-wide detailed field observations, searching for the nests, and genetic monitoring have been undoubtedly justified.

ACKNOWLEDGEMENTS

I am grateful to all members of the Kotkaklubi for their vast effort in collecting data on spotted eagles in Estonia during the last decades, and to all other people who have made their observations available. Jaanus Elts and Andrus Kuus kindly allowed me to use the unpublished data of the second Estonian bird atlas. Asko Lõhmus and Olavi Vainu helped in the compilation of data. Rob Bijlsma and Asko Lõhmus helped to improve the manuscript significantly. The fieldwork and genetic analyses were financed by the Estonian Science Foundation (grants Nos 6050 and 7593), Environmental Investments Fund, and several environmental state bodies in Estonia.

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Konnakotkaste arvukus ja ristumine Eestis hinnatuna otseste vaatluste ning geneetilise analüüsi abil

Ülo Väli

Käesolevas töös kontrolliti, kas Eesti küllalt arvukast, kuid suhteliselt väikese asustustihedusega konnakotka-asurkonnast (10–30 suur-konnakotka, 500–600 väike-konnakotka pesitsusterritooriumi) tehtud otseste vaatluste põhjal eristatud territooriumide koguarv on võrreldav proovialade uurimise abil saadud arvukushinnanguga. Samuti selgitati Eesti hübridiseeruva populatsiooni koosseis, kasutades välimääranguid ja geneetilist analüüsi. Vaatlused aastatel 1991–2010 võimaldasid eristada 664 pesitsusterritooriumi, millest 80,6%-l kohati kotkaid vähemalt kahel aastal. Kindel pesitsemine tuvastati 52,6%-l, tõenäoline pesitsemine 25,6%-l ja võimalik pesitsemine 21,8%-l territooriumidest. 492 territooriumil määrati konnakotkaliik välistunnuste abil ja 158 territooriumil kinnitas määrangut geneetiline analüüs. Suur-konnakotkad asustasid 26 pesitsusterritooriumi, neist 53,8%-l täheldati kindel, 30,8%-l tõenäoline ja 15,4%-l võimalik pesitsemine. Kokku registreeriti kümne suur-konnakotkapaari (neli tõestatud geneetiliste analüüsidega) ja 14 segapaari (12 tõestatud geneetiliselt) pesitsemine, kuid tervelt 12 paari liigiline koosseis muutus, reeglina segapaaride ning väike-konnakotkapaaride suunas; kuuel territooriumil nähti üht suur-konnakotka vanalindu. Uurimisperioodi jooksul jäi vähemalt üheksa suur-konnakotkaterritooriumi asustamata ja kuus asendus väike-konnakotkapaaridega. Kaheksal territooriumil pesitsesid F1-hübriidsed vanalinnud ja viiel hilisema põlvkonna hübriidid. Uuringu tulemused kinnitasid seniseid arvukushinnanguid, kuid näitasid suur-konnakotka ulatuslikku hübridiseerumist ja arvukuse kahanemist. Töö näitab, et mitmetest takistustest hoolimata aitab piisavalt suur vaatluste andmebaas hinnata küllaltki arvuka röövlinnu-asurkonna suurust ja levikut, aga raskesti määratavate ning ristuvate liikide puhul tuleb kindlasti kasutada erimeetodeid, nagu ulatuslik pesade otsimine, detailsete morfoloogiliste kirjelduste kogumine ja geneetiline analüüs.